

AFRL-AFOSR-UK-TR-2014-0036



System-theoretic Interpretation of the Mode Sensing Hypothesis

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EOARD Grant 13-3077

Report Date: 1 August 2014

Final Report for 01 July 2013 to 31 March 2014

Distribution Statement A: Approved for public release distribution is unlimited.

**Air Force Research Laboratory
Air Force Office of Scientific Research
European Office of Aerospace Research and Development
Unit 4515 Box 14, APO AE 09421**

REPORT DOCUMENTATION PAGE				Form Approved OMB No. 0704-0188	
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1. REPORT DATE (DD-MM-YYYY) 1 August 2014		2. REPORT TYPE Final Report		3. DATES COVERED (From – To) 1 July 2013 – 31 March 2014	
4. TITLE AND SUBTITLE System-theoretic Interpretation of the Mode Sensing Hypothesis			5a. CONTRACT NUMBER FA8655-13-1-3077		
			5b. GRANT NUMBER Grant 13-3077		
			5c. PROGRAM ELEMENT NUMBER 61102F		
			5d. PROJECT NUMBER		
6. AUTHOR(S) Prof. Rafal Zbikowski Prof. Graham Taylor			5d. TASK NUMBER		
			5e. WORK UNIT NUMBER		
7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES) Department of Engineering Physics Cranfield University Bedfordshire MK43 0AL UNITED KINGDOM			8. PERFORMING ORGANIZATION REPORT NUMBER N/A		
9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES) EOARD Unit 4515 APO AE 09421-4515			10. SPONSOR/MONITOR'S ACRONYM(S) AFRL/AFOSR/IOE (EOARD)		
			11. SPONSOR/MONITOR'S REPORT NUMBER(S) AFRL-AFOSR-UK-TR-2014-0036		
12. DISTRIBUTION/AVAILABILITY STATEMENT Distribution A: Approved for public release; distribution is unlimited.					
13. SUPPLEMENTARY NOTES					
14. ABSTRACT This document is the Final Performance Report on award no. FA8655-13-1-3077. The stated aim of this research effort was to establish a mathematically precise and biologically meaningful interpretation of the 'Mode Sensing Hypothesis' using system theoretic tools and system identification techniques. The Mode Sensing Hypothesis can be interpreted as the very general proposition that the high performance observed in insect flight can be related to the way in which the insect represents its flight dynamics in the physiological system generating the sensorimotor response which it uses to stabilize its flight. Here we define the sensorimotor response of an insect as the dynamic relationship between the visual, aerodynamic, and inertial stimuli to which the insect responds, and the aerodynamic forces and moments that the insect causes to be exerted in response. This definition accurately captures the classical understanding of what is meant by the term 'sensorimotor response' in the context of flight stabilization and control, but it will be seen that the elaboration of this definition motivates a significant departure from the way in which insect flight control has more recently been modelled.					
15. SUBJECT TERMS EOARD, Mode sensing hypothesis, bio-inspired sensory systems					
16. SECURITY CLASSIFICATION OF:			17. LIMITATION OF ABSTRACT SAR	18. NUMBER OF PAGES 32	19a. NAME OF RESPONSIBLE PERSON Gregg Abate
a. REPORT UNCLAS	b. ABSTRACT UNCLAS	c. THIS PAGE UNCLAS			19b. TELEPHONE NUMBER (Include area code) +44 (0)1895 616021

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Final Report on Award no. FA8655-13-1-3077

Period of Performance: 1 July 2013 to 31 March 2014

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30 June 2014

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1 Summary

This document is the Final Performance Report on award no. FA8655-13-1-3077. The stated aim of this research effort was to establish a mathematically precise and biologically meaningful interpretation of the ‘Mode Sensing Hypothesis’ [1] using system theoretic tools and system identification techniques. The Mode Sensing Hypothesis can be interpreted as the very general proposition that the high performance observed in insect flight can be related to the way in which the insect represents its flight dynamics in the physiological system generating the sensorimotor response which it uses to stabilize its flight [1]. Here we define the sensorimotor response of an insect as the dynamic relationship between the visual, aerodynamic, and inertial stimuli to which the insect responds, and the aerodynamic forces and moments that the insect causes to be exerted in response. This definition accurately captures the classical understanding of what is meant by the term ‘sensorimotor response’ in the context of flight stabilization and control, but it will be seen that the elaboration of this definition motivates a significant departure from the way in which insect flight control has more recently been modelled.

The approach that we adopt here differs from previous, related work in several fundamental respects. One crucial difference is that previous related work has conceptualised the problem of insect flight control by starting with an open-loop description of the insect’s flight dynamics, and postulating closure of the assumed control loop(s) by sensory feedback [2, 3, 4, 5, 6, 7]. This is the same approach as has classically been adopted in aircraft design. However, whereas the empirical engineering approach is able to progress from open-loop wind tunnel studies to test flights with a human pilot, there is obviously no such thing as an open-loop insect. Thus, the underlying ‘plant’ does not really exist except as an abstract theoretical concept, and the only measurable and meaningful reality is that the insect always operates in closed-loop insofar as its own internal feedback pathways are concerned. By this we mean simply that the insect’s internal physiological feedback loops are always operative in flight—even if the normal flight dynamics have been eliminated by tethering. It follows that the only realistic way to approach the problem is from the top down.

Previous system theoretic work on the Mode Sensing Hypothesis has focussed upon the tuning of individually identified optic-flow sensitive visual interneurons [8]. However, flying insects respond to a combination of visual, aerodynamic, and inertial stimuli, and all three kinds of stimulus are generated by the dynamics of the insect’s own self-motion. A key achievement of the present work is the formulation of a state-space model which includes *all* of the visual, aerodynamic, and inertial stimuli to which flying insects are known to respond. Furthermore, rather than being derived from the bottom-up, the model that we present is written in a top-down manner, proceeding from a state-space description of the insect’s sensorimotor response as measured in a tethered flight experiment. The resulting formulation therefore lays the groundwork for future empirical studies, but is also intended to provide fundamental insight into the meaning of a state-space representation of an insect’s sensorimotor response in advance of the significant empirical effort that will be required to fit such a model using the subspace identification methods that we allude to below.

The original exposition of the Mode Sensing Hypothesis [1] attempted—with some success—to relate the modes of motion of the insect’s natural body dynamics to the information carried by individually identified visual interneurons and individually identified descending neurons. In this, its original form, the Mode Sensing Hypothesis was intended to offer a rationale for understanding the design of sensory systems based upon matched filters. However, a weakness of this formulation is that the natural dynamics of the insect (i.e. the dynamics of the uncontrolled system) exist only as an abstract concept, which makes the hypothesis challenging to test empirically. Furthermore, where these natural dynamics have been simulated for model insects, they have been found to be unstable and hence fundamentally different to the stable dynamics of the closed-loop system [9, 10, 4, 6, 7, 11, 12, 13, 14, 15, 16, 17, 18, 19]. Finally, there is an intrinsic

difficulty associated with relating the complex eigenvectors characterising oscillatory modes of motion to meaningful directions in state space.

For this reason, more recent work [8] has sought a more rigorous control theoretic interpretation of the Mode Sensing Hypothesis, developing a framework involving concepts of controllability and observability. However, because controllability and observability are related to the transfer of system energy associated with the input and output of the system, respectively, through its state, the introduction of these concepts begs the question of how the input, output, and state of the system should be defined. Insufficient attention has been paid to this point to date, and a second distinguishing feature of our approach is that by focussing upon the insect's sensorimotor response—a well-defined biological concept—we pin down precisely what is meant by 'input' and 'output' in the context of a system theoretic interpretation of the Mode Sensing Hypothesis. Furthermore, we make the definition of the state space unique by postulating that the function of the insect's sensorimotor response is equitable system energy distribution in the integrated system composed of the sensory and neural processing apparatus, the flight apparatus, and the flight motion dynamics. This postulate of equitable energy distribution is expressed theoretically through the system-theoretic notion of balanced realisation, and is practically important in allowing the identification of a state-space model from experimentally available input-output pairs using the tools and algorithms of subspace system identification.

In summary, this report sets out a framework for formulating an empirically testable control theoretic interpretation of the Mode Sensing Hypothesis. The approach that we take throughout is to juxtapose fundamental theoretical results with biologically meaningful interpretations of those results in the context of an insect's sensorimotor response.

2 Introduction

The aim of this paper is to develop a mathematical framework for modelling the sensorimotor response that insects use to stabilize their flight, defined here as the dynamic relationship between the visual, aerodynamic, and inertial stimuli to which the insect responds, and the aerodynamic forces and moments that the insect causes to be exerted in response. For reasons that we discuss further below, we limit ourselves here to modelling the sensorimotor response with respect to small disturbances from a commanded reference condition of stationary hover. Although it would be possible to extend the model to encompass other reference conditions, there are several advantages to considering this reference condition in particular. First, stationary hover represents an equilibrium flight condition—at least in a time-averaged sense—because the aerodynamic forces and moments must obviously cancel the insect's body weight through the course of a single wingbeat, in order for the insect to remain stationary from one wingbeat to the next. This property becomes important when linearizing the model about the reference condition, because the alternative of linearizing about a non-equilibrium reference condition leads in general to a time-variant system—even if the underlying nonlinear system is time-invariant. Second, because all of the kinematic variables describing the body's motion are zero by default in stationary hover (or can be defined to be so), there is no need to introduce any explicit disturbance notation for these kinematic variables, since their absolute values can be equated directly with their disturbance values. Nevertheless, it is important to keep in mind that the kinematic variables which form the input to the sensorimotor response are to be understood, conceptually at least, as perturbations from a commanded reference condition.

The sensorimotor response of a free-flying insect is the result of a complex interaction between its sensory and neural processing apparatus, its flight apparatus, and its flight motion dynamics. Hence, in theory at least, application of the laws of physics relevant to each of these three subsystems could produce a system of coupled differential equations, which could then be linearized about some biologically plausible reference condition to obtain a linear model of the system. Because such a model would be derived from first principles, it would be expressed in terms of physically meaningful variables, quantified in concrete physical units. Realistically, however,

the classical route of writing out differential equations for the different subsystems and the various couplings between them represents a formidable, and presently insurmountable, challenge. There are several reasons why this is the case. First, even for the most comprehensively-analysed species of flying insect, we lack sufficient knowledge about the structure and function of the animal’s neuromuscular system and flight apparatus to capture this credibly using first-principles modelling. Second, even if such knowledge were available, the first-principles mathematical modelling of the interactions of the neuromuscular system with the physics of flight would still be extraordinarily demanding, even in a simplified perceptual context. Finally, even if such first-principles modelling were to produce a plausible mathematical model, then its validation would require detailed and comprehensive experimental data measured inside a living, flying insect—data that are not likely to be available for some time to come.

An alternative mathematical modelling route, which we propose here, is to derive a *functional*, rather than neuroanatomical, model of the sensorimotor response. For pragmatic reasons, we limit ourselves to using the well-developed theory of linear time-invariant (LTI) systems. This is a powerful framework, which provides not only fundamental insights in control theory, but also operationally feasible algorithms for mathematical modelling [20]. Specifically, we propose an LTI state-space model of the sensorimotor response that could be identified from input-output pairs obtained experimentally, using a subspace system identification method. The experimentally unobservable internal state of the LTI model would be derived by postulating that the function of the insect’s sensorimotor response is equitable system energy distribution in the integrated system composed of the sensory and neural processing apparatus, the flight apparatus, and the flight motion dynamics. This postulate of equitable energy distribution in an LTI system is expressed theoretically through the system-theoretic notion of balanced realisation, and is practically important in allowing the identification of a state-space model from experimentally available input-output pairs using the tools and algorithms of subspace system identification. The main body of the paper aims to specify the form of such a model and to elaborate the mathematical tools that will be needed for its analysis. We conclude by using the model to facilitate a system theoretic interpretation of the Mode Sensing Hypothesis, which in its most general form is the proposition that the high performance observed in insect flight can be related to the way in which the insect represents its flight dynamics in the physiological system generating its sensorimotor response [1].

3 Linear time-invariant systems theory

The causal relationship between sensory input and motor output is a dynamic one. That is to say, both input and output are functions of time, which cannot be eliminated to obtain a static input-output curve. Instead, the optomotor response of a flying insect has to be expressed as a dynamic relationship $\mathcal{L}: \mathbf{u}(t) \rightarrow \mathbf{y}(t)$ between two functions of continuous time t . This relationship is fully expressed by the set of all input-output pairs, each pair being composed of an input $\mathbf{u}(t)$, and its corresponding output $\mathbf{y}(t)$, defined on the time interval $(-\infty, \infty)$. In practice, it is only possible to measure a subset of possible input-output pairs empirically, and only over a finite time interval. A fundamental question, therefore, is whether there exists a mathematical model which, for *any* input $\mathbf{u}(t)$, allows us to predict the corresponding output $\mathbf{y}(t)$? The answer is affirmative for an LTI system, so we begin by asking whether it is reasonable to model the sensorimotor responses of flying insects in this way. Of course, no real physical system is either strictly linear or strictly time-invariant, so that the LTI framework always represents something of a theoretical idealisation. Nevertheless, LTI systems theory has proven to be an exceedingly useful framework for modelling control problems in engineering, and has also found extensive use in biology. Thus, the important question is not whether insect sensorimotor responses are actually linear and time-invariant—which they are not—but rather whether there are reasons for thinking that they may be modelled as such under a restricted set of conditions. In order to answer this question, we

must first define what we mean by ‘input’ and ‘output’ in the context of an insect’s sensorimotor response.

3.1 Input-output description of an insect’s sensorimotor response

We define the sensorimotor response of a flying insect as the input-output relationship $\mathcal{L}: \mathbf{u}(t) \rightarrow \mathbf{y}(t)$ between the external stimuli to which the insect responds, and the aerodynamic forces and moments that the insect causes to be exerted in response. In principle, the aerodynamic forces and moments could be measured directly using a force-moment balance in tethered flight, or indirectly using estimates of body acceleration obtained in free flight. In either case, by ‘output’, we mean the 6×1 vector:

$$\mathbf{y} = \begin{bmatrix} \Delta \mathbf{F} \\ \Delta \mathbf{M} \end{bmatrix} \stackrel{\text{def}}{=} \begin{bmatrix} \mathbf{F} - \mathbf{F}_r \\ \mathbf{M} - \mathbf{M}_r \end{bmatrix} \quad (1)$$

where \mathbf{F} and \mathbf{M} are 3×1 vectors of aerodynamic force and moment components, respectively, and where \mathbf{F}_r and \mathbf{M}_r represent their reference values in some specified reference condition, which we take here to be a condition of stationary hover. For convenience, we will assume that the aerodynamic forces and moments are resolved in a right-handed set of body axes $\{x_b, y_b, z_b\}$ with their origin at the time-averaged position of the insect’s centre of mass, and with their y_b -axis normal to the insect’s plane of symmetry. The direction of the x_b - and z_b -axes may be fixed arbitrarily in the $x_b z_b$ -plane, but we will assume that the x_b -axis points in an anterior direction.

By ‘input’, we mean the information needed to describe any stimulus simulating the effects of an externally-imposed rotation and/or translation of the insect’s body with respect to some external frame of reference. Insects respond to a combination of visual, aerodynamic, and inertial stimuli, and we will therefore need to define a separate frame of reference for each. Thus, we will define a visual frame of reference (\mathcal{F}_v) that is fixed with respect to the surrounding visual environment, an aerodynamic frame of reference (\mathcal{F}_a) that is fixed with respect to the surrounding mass of air, and an inertial frame of reference (\mathcal{F}_i) that for practical purposes may be assumed to be fixed with respect to the Earth. All of the inputs that we specify will be measured in the insect’s body axes $\{x_b, y_b, z_b\}$, which we will take to define a fourth frame of reference \mathcal{F}_b . We will use an obvious subscript notation to indicate to which frame of reference a given kinematic variable refers, and with respect to which frame of reference it is being measured. Thus, the notation $\mathbf{v}_{b|v}$ will be used to refer to the velocity of the body frame of reference \mathcal{F}_b with respect to the visual frame of reference \mathcal{F}_v .

Concerning visual stimuli, flying insects respond strongly to rotational and translational optic flow, which they sense using their compound eyes [1]. Insects will also orientate themselves with respect to luminance gradients in the visual environment, which they sense using their compound eyes and ocelli [1]. We will assume that the visual environment is rigid, and will further assume that the distance between the insect and the visual scene remains constant in all directions in the visual frame of reference \mathcal{F}_v . This assumption is satisfied by any visual stimulus simulating pure rotational self-motion, and by any visual stimulus simulating translation through a visual scene in which the normal to every visible surface is perpendicular to the direction of translational self-motion. Abstract examples of the latter include flight at a constant altitude over an infinite horizontal plane, and flight parallel to the long axis of an infinitely long cylinder. The significance of this assumption is that it keeps the input vector finite-dimensional, by avoiding the need to keep separate track of the distance to every point within the visual scene. Under these assumptions, the external visual stimulus in a given environment is determined at every instant by the velocity ($\mathbf{v}_{b|v}$) and angular velocity ($\boldsymbol{\omega}_{b|v}$), of the body frame of reference \mathcal{F}_b with respect to the visual frame of reference \mathcal{F}_v , and by the Euler angles $\boldsymbol{\phi}_{b|v}$ of the body axes $\{x_b, y_b, z_b\}$ within a set of visual axes $\{x_v, y_v, z_v\}$. The z_v -axis will be assumed to coincide with the principal axis of any variation in luminance, but the x_v - and y_v -axes may be fixed arbitrarily within the $x_v y_v$ -plane.

With regard to the external aerodynamic stimuli that the insect receives, flying insects are known to respond to both the speed and direction of the local flow, which they sense using their flow-sensitive hairs and antennae [1]. In the interests of keeping the input vector finite

dimensional, we will assume as a first approximation that the external aerodynamic stimulus is determined at every instant by the velocity ($\mathbf{v}_{b|a}$) and angular velocity ($\boldsymbol{\omega}_{b|a}$) of the body frame of reference \mathcal{F}_b with respect to the aerodynamic frame of reference \mathcal{F}_a . The reality is more complicated than this, because the local flow in the vicinity of the insect is expected to be unsteady. However, the most important source of aerodynamic unsteadiness will be the periodicity of the flow induced by the insect's own wingbeat, which can be handled separately if necessary within a time-periodic modelling framework. Finally, with regard to inertial stimuli, flying insects are known to respond to their angular velocity, and perhaps also to their angular acceleration, which they sense using a variety of different mechanisms [1]. Including the angular acceleration as an input causes difficulties later in the free-flight case, and although these can be handled if required, we choose here to simplify the presentation by assuming that the inertial stimulus is determined at every instant by the angular velocity ($\boldsymbol{\omega}_{b|i}$) of the body frame of reference \mathcal{F}_b with respect to the inertial frame of reference \mathcal{F}_i .

It follows that we may specify any given input as the 18×1 vector:

$$\mathbf{u} = \begin{bmatrix} \mathbf{v}_{b|v} \\ \boldsymbol{\omega}_{b|v} \\ \dots \\ \boldsymbol{\phi}_{b|v} \\ \mathbf{v}_{b|a} \\ \boldsymbol{\omega}_{b|a} \\ \dots \\ \boldsymbol{\omega}_{b|i} \end{bmatrix} \quad (2)$$

where each of the entries in bold represents a 3×1 vector. We will use the freedom that we have in fixing the x_b - and z_b -axes, and the x_v - and y_v -axes, to align the body axes $\{x_b, y_b, z_b\}$ with the visual axes $\{x_v, y_v, z_v\}$ in the reference condition of stationary hover. With this restriction, the input vector \mathbf{u} is identically zero in the assumed reference condition, and it follows that the disturbance values of all of the input variables are the same as the absolute values of those variables. For ease of explanation, we have partitioned the input vector \mathbf{u} into four blocks defining the optic flow stimulus, the luminance gradient stimulus, the aerodynamic stimulus, and the inertial stimulus, respectively. We now consider whether it may be reasonable to treat the insect's response to these different kinds of stimuli as being uncoupled, which is a necessary condition for assuming linearity.

3.2 Linearity

A system is said to be linear if all of its input-output pairs obey the superposition principle. This means that if an input $\mathbf{u}_1(t)$ results in the output $\mathbf{y}_1(t)$, and if an input $\mathbf{u}_2(t)$ results in the output $\mathbf{y}_2(t)$, then any linear combination of both inputs will result in the same linear combination of both outputs. Thus, for a system described by a linear dynamic relationship \mathcal{L} , any weighted sum of inputs $a_1\mathbf{u}_1(t) + a_2\mathbf{u}_2(t)$, where a_1 and a_2 are scalar weights, will produce the output:

$$\mathcal{L}[a_1\mathbf{u}_1(t) + a_2\mathbf{u}_2(t)] = a_1 \overbrace{\mathcal{L}[\mathbf{u}_1(t)]}^{\mathbf{y}_1(t)} + a_2 \overbrace{\mathcal{L}[\mathbf{u}_2(t)]}^{\mathbf{y}_2(t)} \quad (3)$$

It follows that we may only model an insect's sensorimotor response using LTI systems theory if we can assume that the insect's responses to optic flow stimuli, luminance intensity stimuli, aerodynamic stimuli, and inertial stimuli are uncoupled. This can be seen, for example, by letting:

$$\mathbf{u}_1 = \begin{bmatrix} \mathbf{v}_{b|v} \\ \boldsymbol{\omega}_{b|v} \\ \dots \\ \mathbf{0} \\ \mathbf{0} \\ \dots \\ \mathbf{0} \end{bmatrix} \quad \mathbf{u}_2 = \begin{bmatrix} \mathbf{0} \\ \mathbf{0} \\ \dots \\ \boldsymbol{\phi}_{b|v} \\ \mathbf{0} \\ \dots \\ \mathbf{0} \end{bmatrix} \quad (4)$$

such that $\mathcal{L}[\mathbf{u}_1(t)]$ represents the so-called ‘optomotor response’ to optic flow stimuli, and $\mathcal{L}[\mathbf{u}_2(t)]$ represents the so-called ‘dorsal light response’ to the luminance gradient. Then, by Eq. 3, the superposition principle requires that $\mathcal{L}[\mathbf{u}_1(t) + \mathbf{u}_2(t)] = \mathcal{L}[\mathbf{u}_1(t)] + \mathcal{L}[\mathbf{u}_2(t)]$, which is true in general if and only if the optomotor response and the dorsal light response are uncoupled. The same reasoning holds for any other combination of stimuli, including of course where \mathbf{u}_1 and \mathbf{u}_2 are taken to represent the same kind of stimulus.

In light of this, we will state as our working assumption that the insect’s responses to different stimuli are uncoupled, so that they combine in an additive manner. This is certainly not true in a literal sense, because some responses are known to gate others. However, the very fact that biologists have coined different names for different components of the sensorimotor response is itself a reflection of the fact that it has long been thought reasonable to study these responses independently—a tradition that we continue here. More significantly, perhaps, Eq. 3 requires that $\mathcal{L}[a_1\mathbf{u}_1(t)] = a_1\mathcal{L}[\mathbf{u}_1]$, and hence that the output of a linear system should scale in proportion to its input. It follows that a linear model of an insect’s sensorimotor response can only possibly be valid over a certain range—not least because motor output cannot increase indefinitely with increases in input amplitude. Saturation nonlinearities are not peculiar to insects, of course, being characteristic of any system with finite energy, but there are some specific nonlinearities in the sensorimotor pathways of insects that merit further consideration here.

Motion vision in insects is founded upon the detection of moving contrast by neural circuits known as elementary movement detectors. Flies and other insects use correlation-type motion detectors, which detect local motion of the visual scene by comparing the luminance at one point in the visual field to the luminance at an adjacent point a few milliseconds earlier. The output of such a detector depends upon the pattern of contrast in the visual scene, but the resulting nonlinearities will average out when analysing a natural visual scene containing many spatial frequencies. More importantly, whereas the output of a correlation-type motion detector increases monotonically with the local angular velocity of the visual scene at low speeds, it falls off at higher speeds. This is because the output is maximal at an angular velocity equal to the angular spacing of the points at which the luminance is compared, divided by the delay between the times at which the luminance is sampled at the two locations. It follows that a linear model of the optomotor response can only be expected to perform well over a certain range of angular velocity of the visual scene. With this in mind, the entries of the input vector in a linear model of the insect’s sensorimotor response must necessarily represent not merely disturbances, but *small* disturbances from the reference condition of stationary hover.

3.3 Time invariance

A linear system is said to be time-invariant if the dynamic relationship \mathcal{L} mapping input to output does not change with time. Thus, if it is shown that a particular input $\mathbf{u}_0(t)$ results in the output $\mathbf{y}_0(t)$, then the same input time-shifted by Δt will result in the output $\mathbf{y}_0(t + \Delta t)$, such that:

$$\mathcal{L}[\mathbf{u}_0(t + \Delta t)] = \mathbf{y}_0(t + \Delta t) \quad (5)$$

Time invariance therefore entails strict repeatability, which is unlikely to hold for any complex biological system: the dynamics of the sensorimotor system will vary, for example, with the physiological state of the insect. Nevertheless, provided that the dynamics of this variation are much slower than the dynamics of the sensorimotor response itself—which is certainly the case for physiological variation mediated by flight hormones such as octopamine—then the time-variance of the relationship will have an essentially static effect upon its own dynamics. This being so, the main complication that follows is the statistical one of controlling for variation between measured input-output pairs through some appropriate form of model averaging.

A second, quite separate, source of time-variance is the periodicity of the wingbeat itself [3]. This periodicity means that the dynamics of the sensorimotor response are fundamentally time-periodic. On the other hand, it is an open question whether or not this periodicity is important

and therefore needs to be captured in the model. What matters here is whether the periodicity of the sensorimotor response has any appreciable impact upon the flight dynamics that it controls. The answer to this question again hinges upon timescale. Specifically, if the wingbeat period is comparable to any of the characteristic timescales of the insect’s rigid body motions, then the insect’s flight dynamics will also be fundamentally time-periodic, and it will be necessary to account explicitly for the periodicity of the aerodynamic forces and moments when modelling the insect’s sensorimotor response. Methods for doing so are available within the state space modelling framework that we now consider, and have already been applied successfully in the context of insect flight dynamics and control [17]. However, to simplify the presentation here, we will assume that we are dealing with an insect in which the wingbeat frequency is sufficiently high that the periodicity of the aerodynamic forces and moments does not manifest itself in the insect’s flight dynamics [17].

If the wingbeat period is much shorter than the shortest characteristic timescale of the insect’s rigid body motions, then the insect’s flight dynamics will be essentially unaffected by the periodicity of its sensorimotor response [2]. Then, although the flight forces themselves will be time-periodic, their effect upon the flight dynamics will depend upon their time-average over one or more wingbeats. This being so, it should be possible to ignore the periodic component of the insect’s sensorimotor response without losing any important information from the perspective of flight stabilization and control. In this case, the sensorimotor response may be treated as being time-invariant from the perspective of the flight dynamics that it controls. An important corollary, therefore, is that *any* LTI model of an insect’s sensorimotor response will be frequency-limited of necessity, because the time-invariance of the model limits us to considering timescales that are much longer than the wingbeat period, but much shorter than any physiological fluctuations in the sensorimotor response. These limits upon bandwidth will have some important and useful implications later for the modelling and identification framework that we adopt.

4 Linear time-invariant modelling framework

Using an LTI modelling framework to describe an insect’s sensorimotor response amounts to seeking an expression for \mathcal{L} such that for *any* input stimulus $\mathbf{u}(t)$, the corresponding force-moment output $\mathbf{y}(t)$ is produced by $\mathbf{y}(t) = \mathcal{L}[\mathbf{u}(t)]$, where \mathcal{L} obeys Eqs. 3 and 5 above. This is known as an external description of the system, and is attractive inasmuch as it relates sensory input to motor output in a direct fashion. Unfortunately, the simplicity of the statement $\mathbf{y}(t) = \mathcal{L}[\mathbf{u}(t)]$ belies the complexity of the underlying problem. Because the input $\mathbf{u}(t)$ and output $\mathbf{y}(t)$ are both functions of continuous time, they both require infinitely many numbers for their full description—even if time t belongs to a finite interval. Hence, the LTI relationship \mathcal{L} associates an infinite-dimensional object $\mathbf{y}(t)$, the output, with an infinite-dimensional object $\mathbf{u}(t)$, the input. Thus, the LTI relationship \mathcal{L} is itself infinite dimensional.

4.1 External LTI description: input-output relationship

For a causal LTI system with inputs satisfying:

$$\mathbf{u}(t) = \mathbf{0}, \quad t < 0 \quad (6)$$

it can be shown that \mathcal{L} is an integral infinite-dimensional operator given by:

$$\mathbf{y}(t) \stackrel{\text{def}}{=} \mathcal{L}[\mathbf{u}(t)] = \int_0^t \mathbf{h}(t - \tau) \mathbf{u}(\tau) d\tau, \quad (7)$$

where \mathbf{h} denotes the impulse response of the system, defined as the output that the system produces in response to an input comprising a unit impulse at time zero (i.e. Dirac’s delta). Unfortunately, although the integral operator \mathcal{L} mapping $\mathbf{u}(t)$ to $\mathbf{y}(t)$ is fully defined when the impulse

response \mathbf{h} is known, acquiring this knowledge is not straightforward, because the impulse response \mathbf{h} is an infinite-dimensional object. A theoretically insightful and practically useful way around that difficulty is not to try to represent the LTI operator \mathcal{L} directly with \mathbf{h} , but to express \mathcal{L} indirectly with an auxiliary set of differential equations. This indirect approach leads to an internal LTI model, or state-space model, which is the form we will adopt here.

4.2 Internal LTI description: state-space model

For p inputs collected in the input vector \mathbf{u} , and q outputs collected in the output vector \mathbf{y} , the internal LTI model is assumed to have n internal states collected in the state vector \mathbf{x} . With these assumptions, the external LTI model expressed by Eq. 7 can be derived from the following system of equations:

$$\dot{\mathbf{x}}(t) = \mathbf{A}\mathbf{x}(t) + \mathbf{B}\mathbf{u}(t), \quad \mathbf{x}(0) = \mathbf{x}_0, \quad (8)$$

$$\mathbf{y}(t) = \mathbf{C}\mathbf{x}(t) + \mathbf{D}\mathbf{u}(t). \quad (9)$$

where $\dot{\mathbf{x}}$ stands for differentiation of \mathbf{x} with respect to time t . The Jacobian matrices \mathbf{A} , \mathbf{B} , \mathbf{C} , \mathbf{D} have constant, real entries and dimensions $n \times n$, $n \times p$, $q \times n$, $q \times p$, respectively. Eqs. 8–9 are linear, and the constancy of the matrices \mathbf{A} , \mathbf{B} , \mathbf{C} , and \mathbf{D} means that they are also time-invariant. Eqs. 8–9 are therefore known as an internal LTI model, or state-space model, of the system.

4.3 Correspondence between the internal and external LTI descriptions

The external description of the system in Eq. 7 can be derived from the internal description of the system in Eqs. 8–9 as follows. The solution obtained by integrating Eq. 8 for the initial condition \mathbf{x}_0 is well known:

$$\mathbf{x}(t) = e^{\mathbf{A}t} \mathbf{x}_0 + \int_0^t e^{\mathbf{A}(t-\tau)} \mathbf{B}\mathbf{u}(\tau) d\tau \quad (10)$$

Substituting Eq. 10 into Eq. 9 yields the convolution equation:

$$\mathbf{y}(t) = \mathbf{C}e^{\mathbf{A}t} \mathbf{x}_0 + \int_0^t \mathbf{C}e^{\mathbf{A}(t-\tau)} \mathbf{B}\mathbf{u}(\tau) d\tau + \mathbf{D}\mathbf{u}(t) \quad (11)$$

from which it is clear that the response of the system may be decomposed into two parts: the zero-input response, obtained by setting $\mathbf{u}(t) = \mathbf{0}$ for $t \geq 0$ in Eq. 11; and the zero-state response, obtained by setting $\mathbf{x}_0 = \mathbf{0}$ in Eq. 11. The total response of the system comprises the sum of the zero-input response, corresponding to the first term on the right hand side of Eq. 11, and the zero-state response, corresponding to the second and third terms on the right hand side of Eq. 11.

The impulse response of the system, \mathbf{h} , is simply the zero-state response of the system when presented with a unit impulse at time zero. Hence, using $\delta(t)$ to denote the $p \times 1$ vector of Dirac's deltas, the impulse response is obtained by setting $\mathbf{x}_0 = \mathbf{0}$ and $\mathbf{u}(t) = \delta(t)$ in Eq. 11, and integrating to yield:

$$\mathbf{h}(t - \tau) = \int_0^t \mathbf{C}e^{\mathbf{A}(t-\tau)} \mathbf{B}\delta(\tau) d\tau + \mathbf{D}\delta(t) \quad (12)$$

$$= \mathbf{C}e^{\mathbf{A}(t-\tau)} \mathbf{B} + \mathbf{D}\delta(t) \quad (13)$$

where we have made use of the fact that $\delta(t)$ is zero for all $t \neq 0$, and has the property that its integral is identically 1. Substituting Eq. 13 back in to Eq. 11 yields:

$$\mathbf{y}(t) = \mathbf{C}e^{\mathbf{A}t} \mathbf{x}_0 + \int_0^t \mathbf{h}(t - \tau) \mathbf{u}(\tau) d\tau \quad (14)$$

which differs from Eq. 7 in that Eq. 14 includes the zero-input response of the system. Hence, it is implicit in the external description of Eq. 14 that $\mathbf{x}_0 = \mathbf{0}$ (in which case the system is said to be relaxed at time $t = 0$). With this restriction, the internal LTI model in Eqs. 8–9 leads directly to the external LTI model in Eq. 7.

4.4 Meaning of the state-space description

The internal LTI model (Eqs. 8–9) has several advantages over the external LTI model (Eq. 7) to which it leads: first, it is finite-dimensional; second, it is explicitly parameterised by a fixed number of constants corresponding to the entries of matrices \mathbf{A} , \mathbf{B} , \mathbf{C} , and \mathbf{D} ; third, it yields an exact solution for the output (Eq. 11); and fourth, it represents the impulse response explicitly (Eq. 13). These properties make the state-space description in Eqs. 8–9 a theoretically and practically attractive alternative to the abstract operator formulation in Eq. 7. In order to make use of it, however, we must first address a fundamental and non-trivial question: What is the meaning of the state vector \mathbf{x} , and what is the significance of its initial condition \mathbf{x}_0 ?

Formally, the state vector \mathbf{x} provides the *minimal* information about the system that is needed to determine its future output, assuming that future inputs can be observed [21]. The dimension n of the state vector \mathbf{x} is a precise expression of this minimality, corresponding to the *smallest* number of internal states needed to determine the future behaviour of the system. This intuitively appealing requirement is made precise within the LTI framework. Eq. 8 connects the input \mathbf{u} and state \mathbf{x} with the rate of change in state $\dot{\mathbf{x}}$, and its solution (Eq. 10) therefore allows prediction of the future state of the system, under input \mathbf{u} for initial condition \mathbf{x}_0 . Hence, the state vector \mathbf{x} must contain a set of internal states which predictably determines the transfer of input energy to output energy through the system’s dynamics. The initial condition of the state vector \mathbf{x}_0 determines the internal energy of the system accumulated over the interval $(-\infty, 0)$, and effectively summarises the system’s integrated time history before the input $\mathbf{u}(t)$ is applied at $t \geq 0$. A system for which $\mathbf{x}_0 = \mathbf{0}$ has no internal energy, and hence no tendency to change state until a non-zero input is applied, as can be seen by inspection of Eq. 10. It follows that any non-zero elements of the state vector \mathbf{x} can be thought of as representing disturbances from the equilibrium point associated with the zero-input condition $\mathbf{u}(t) = \mathbf{0}$. Thus, if we assume for convenience that the zero-input condition produces a steady state of hover, then the elements of the state vector \mathbf{x} specifically represent disturbances from the equilibrium associated with hovering flight.

5 Sensorimotor response in tethered flight

Having discussed the meaning of the state-space description in general terms, we now expand upon this for the case of the sensorimotor response recorded in tethered flight. The importance of expanding the model in this way is that it will allow us to explore the physical and biological meaning of the otherwise abstract state-space representation in Eqs. 8–9. Our reason for focusing upon this paradigm is that the design of a tethered flight experiment corresponds naturally to the definition of a sensorimotor response as the relationship between the external stimuli to which the insect responds, and the aerodynamic forces and moments that the insect causes to be exerted in response. That is to say, the input vector \mathbf{u} in a tethered flight experiment is defined as the information determining the visual, aerodynamic, or inertial stimulus with which the insect is provided. Likewise, the output vector \mathbf{y} is known directly from the vector of forces and moments that the insect exerts upon its tether. Although input and output can be defined similarly in a free-flight experiment, the stimuli that are provided at the input combine with the insect’s own self-motion to determine the stimulus that the insect actually observes, whilst the forces and moments have to be inferred indirectly from measurements of the flight kinematics. It is therefore simpler—both practically and conceptually—to consider the tethered flight case first.

5.1 Meaning of the direct transmission matrix

Having already specified the output vector \mathbf{y} and input vector \mathbf{u} in Eqs. 1–2 above, we begin by considering the elements of the matrix \mathbf{D} . This term, sometimes called the direct transmission matrix, describes the direct transfer of energy from input to output, exclusive of the dynamics of the sensorimotor response proper. Given that we have defined the output as the aerodynamic

forces and moments, it is self-evident that direct transfer of energy from input to output can only possibly be expected to occur in respect of the aerodynamic inputs. These aerodynamic inputs are expected to affect the aerodynamic forces and moments acting upon the insect's wings and body—even if the insect makes no change to its motor commands. However, it will only be reasonable to model this effect as a direct transfer of energy from input to output if the aerodynamic forces and moments are linearly dependent upon the aerodynamic velocity $\mathbf{v}_{b|a}$ and angular velocity $\boldsymbol{\omega}_{b|a}$ at that instant. This linear dependence will not hold for the general case of an unsteady flow, or in respect of large changes in airspeed or angle of attack, but it should represent a reasonable first approximation in the case of slow or small-amplitude motions. This being so, the only non-zero elements of the Jacobian matrix \mathbf{D} must correspond to the partial derivatives of the aerodynamic forces and moments with respect to $\mathbf{v}_{b|a}$ and $\boldsymbol{\omega}_{b|a}$, at the reference condition, in the hypothetical case that the insect makes no change to its motor commands. Although there is no reason why these aerodynamic derivatives must be known in advance of any empirical investigation, it may be noted that they are precisely the same aerodynamic derivatives as have been computed numerically in a series of recent papers on insect flight stability [9, 10, 4, 6, 7, 11, 12, 13, 14, 15, 16, 17, 18, 19].

5.2 Meaning of the state vector

Whereas we were able to specify the elements of the input vector \mathbf{u} and output vector \mathbf{y} from first principles, the complete set of internal states contained in the state vector \mathbf{x} cannot be determined in this way. This is because any set of internal states sufficient to determine the transfer of energy from input to output through the dynamics of the insect's sensorimotor response will include an *a priori* unknown number of physiological states involved in the sensor dynamics, processing dynamics, and actuator dynamics. Nevertheless, it is still possible to specify a subset of the internal states from first principles, because the state vector \mathbf{x} must necessarily contain *all* of the kinematic information needed to relate the stimulus that the insect's sensors receive to the stimulus contained in the input vector \mathbf{u} . The reason why these stimuli are not the same is that most of the sensors involved in flight control are located on the head, which rotates with respect to the body. We will therefore have cause to define a right-handed set of head axes $\{x_h, y_h, z_h\}$ with their origin at the neck joint, their y_h -axis normal to the head's plane of symmetry, and their x_h - and z_h -axes defined so as to be parallel to the x_b -axis and z_b -axes of the body in the reference condition about which the model is linearized. We will take these axes to define a head-fixed frame of reference (\mathcal{F}_h).

The relative orientation of the head and body is of central importance in making sense of the self-motion stimuli that the sensors on the head receive, so the information needed to specify the orientation of the head must obviously feature somehow in the state vector \mathbf{x} . Having resolved all of the other kinematic variables in the body axes $\{x_b, y_b, z_b\}$, it will prove convenient to specify the relative orientation of head using a set of Euler angles ($\boldsymbol{\phi}_{b|h}$) giving the orientation of the body axes $\{x_b, y_b, z_b\}$ with respect to the head axes $\{x_h, y_h, z_h\}$. Likewise, we will specify the relative angular velocity of the head by defining the angular velocity $\boldsymbol{\omega}_{b|h}$ of the body frame of reference \mathcal{F}_b with respect to the head frame of reference \mathcal{F}_h . We note that the angular velocity of the head with respect to the body ($\boldsymbol{\omega}_{h|b} = -\boldsymbol{\omega}_{b|h}$) will sum with the angular velocity of the body with respect to any of the other frames of reference that we have defined, to determine the visual, aerodynamic, and inertial stimuli experienced by head-mounted sensors such as the compound eyes and the antennae. Thus, we may write the $n \times 1$ state vector as:

$$\mathbf{x} = \begin{bmatrix} \boldsymbol{\omega}_{b|h} \\ \boldsymbol{\phi}_{b|h} \\ \mathbf{z} \end{bmatrix} \quad (15)$$

where \mathbf{z} is an $r \times 1$ vector of physiological states, with $r = n - 6$. In the event that it were necessary to model the time-periodic component of the insect's sensorimotor response, the state

vector \mathbf{x} would also include wingbeat phase as a state of the system, but we do not pursue this complication further here.

5.3 State-space model of the sensorimotor response in tethered flight

We are now in a position to write down an expanded version of the generic state-space model in Eqs. 8–9 corresponding to the sensorimotor response in tethered flight. Many of the elements of the Jacobian matrices \mathbf{A} , \mathbf{B} , \mathbf{C} , \mathbf{D} will be identically zero, and our approach will therefore be to express the state-space equations in an expanded form in which we write any non-zero elements of the Jacobian matrices as $\mathbf{A}_{11} \dots \mathbf{A}_{33}$, etc. We will explain the sparse structure of these matrices shortly, but with this notation, the state-space model of the sensorimotor response in tethered flight may be expanded as follows:

$$\begin{bmatrix} \dot{\omega}_{b|h} \\ \dot{\phi}_{b|h} \\ \dot{\mathbf{z}} \end{bmatrix} = \begin{bmatrix} \mathbf{A}_{11} & \mathbf{A}_{12} & \mathbf{A}_{13} \\ \mathbf{I} & \mathbf{0} & \mathbf{0} \\ \mathbf{A}_{31} & \mathbf{A}_{32} & \mathbf{A}_{33} \end{bmatrix} \begin{bmatrix} \omega_{b|h} \\ \phi_{b|h} \\ \mathbf{z} \end{bmatrix} + \begin{bmatrix} \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{B}_{14} & \mathbf{B}_{15} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{B}_{31} & \mathbf{B}_{32} & \mathbf{B}_{33} & \mathbf{B}_{34} & \mathbf{B}_{35} & \mathbf{B}_{36} \end{bmatrix} \begin{bmatrix} v_{b|v} \\ \omega_{b|v} \\ \phi_{b|v} \\ v_{b|a} \\ \omega_{b|a} \\ \omega_{b|i} \end{bmatrix} \quad (16)$$

$$\begin{bmatrix} \Delta \mathbf{F} \\ \Delta \mathbf{M} \end{bmatrix} = \begin{bmatrix} \mathbf{0} & \mathbf{0} & \mathbf{C}_{13} \\ \mathbf{0} & \mathbf{0} & \mathbf{C}_{23} \end{bmatrix} \begin{bmatrix} \omega_{b|h} \\ \phi_{b|h} \\ \mathbf{z} \end{bmatrix} + \begin{bmatrix} \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{D}_{14} & \mathbf{D}_{15} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{D}_{24} & \mathbf{D}_{25} & \mathbf{0} \end{bmatrix} \begin{bmatrix} v_{b|v} \\ \omega_{b|v} \\ \phi_{b|v} \\ v_{b|a} \\ \omega_{b|a} \\ \omega_{b|i} \end{bmatrix} \quad (17)$$

where \mathbf{I} denotes the 3×3 identity matrix. The entries $\mathbf{A}_{11} \dots \mathbf{A}_{13}$, \mathbf{B}_{14} , \mathbf{B}_{15} , and $\mathbf{D}_{14} \dots \mathbf{D}_{25}$ are 3×3 matrices; \mathbf{A}_{31} , \mathbf{A}_{32} , and $\mathbf{B}_{31} \dots \mathbf{B}_{36}$ are $r \times 3$ matrices; \mathbf{C}_{13} and \mathbf{C}_{23} are $3 \times r$ matrices; \mathbf{A}_{33} is an $r \times r$ matrix. We now explain the structure and meaning of each of the Jacobian matrices.

Beginning with Eq. 16, the \mathbf{A} matrix characterises how the state \mathbf{x} evolves independent of the input \mathbf{u} , whilst the matrix \mathbf{B} characterises the transfer of energy from the input \mathbf{u} to the state \mathbf{x} . Hence, because almost nothing can be said from first principles about the specific meaning of the system state \mathbf{x} , rather little can be said about most of the entries of \mathbf{A} and \mathbf{B} . Nevertheless, it is obvious from first principles that the visual inputs in the first two blocks of the input vector \mathbf{u} can only possibly affect the head kinematics by modifying the internal physiological state of the system \mathbf{z} . Consequently, the entries of \mathbf{B} which represent the partial derivatives of $\dot{\phi}_{b|h}$ with respect to the visual stimuli must all be zero. Likewise, the zero entries in the second row matrix \mathbf{A} and matrix \mathbf{B} are easily understood by considering the kinematic relationship between the rate of change in the Euler angles of the body with respect to the head ($\dot{\phi}_{b|h}$), and the angular velocity of the body with respect to the head ($\omega_{b|h}$). Because we have assumed that $\phi_{b|h}$ and $\omega_{b|h}$ are identically zero in the reference condition about which the model is linearized, this kinematic relationship has the unusually simple form:

$$\dot{\phi}_{b|h} = \omega_{b|h} \quad (18)$$

which explains why the only non-zero entry in the middle row of the \mathbf{A} and \mathbf{B} matrices in Eq. 16 is the identity matrix \mathbf{I} appearing in the first column of \mathbf{A} . The remaining non-zero entries of the matrices \mathbf{A} and \mathbf{B} cannot be determined from first principles, and must instead be identified empirically from experimentally measured input-output pairs.

The matrix \mathbf{C} describes the transfer of system energy from the state \mathbf{x} to the output \mathbf{y} . Eq. 17 shows \mathbf{C}_{13} and \mathbf{C}_{23} as the only non-zero elements of this matrix. These $3 \times r$ matrices describe the transfer of system energy to output energy through the internal physiological state of the system (\mathbf{z}), and are likely to be of rather high dimension. The remaining entries in \mathbf{C} represent

the partial derivatives of the aerodynamic forces and moments with respect to the orientation ($\phi_{b|h}$) and angular velocity ($\omega_{b|h}$) of the body relative to the head, at the reference condition. We have assumed that these partial derivatives are negligible, and hence zero, on the grounds that the aerodynamic forces and moments acting upon the head will be small in comparison with those acting upon the wings and body. Concerning the direct transmission matrix \mathbf{D} , the non-zero submatrices $\mathbf{D}_{14} \dots \mathbf{D}_{25}$ represent the partial derivatives of the aerodynamic forces and moments with respect to the aerodynamic velocity ($v_{b|a}$) and angular velocity ($\omega_{b|a}$) of the body, at the reference condition, in the hypothetical case that the insect makes no change to its motor commands. For reasons that we have already discussed, these are the only non-zero elements of the direct transmission matrix \mathbf{D} (see Section 5.1).

5.4 Summary

Although the state-space model in Eqs. 16–17 was derived for a tethered flight experiment paradigm, it nevertheless characterises a meaningful biological system. That is to say, although the model includes none of the flight dynamics, it does encapsulate all of the sensor dynamics, processing dynamics, and actuator dynamics of a flying insect, together with the multi-body dynamics that are involved in the insect’s head movements. In principle, a state-space model of this sort can be identified from experimentally determined pairs of inputs $\mathbf{u}(t)$ and outputs $\mathbf{y}(t)$ using the techniques of subspace system identification. In particular, the algorithms of the Subspace Identification Methods (SIM) software package [22], [23] provide well understood, effective, reliable and practical tools for establishing the state vector $\mathbf{x}(t)$ and the undetermined elements of the corresponding system matrices \mathbf{A} , \mathbf{B} , \mathbf{C} , \mathbf{D} empirically. Furthermore, the SIM software produces an estimate of the minimal size n of the state to within a user-prescribed modelling accuracy. Thus, having written down the model in Eqs. 16–17, it is reasonable to suppose that it may be possible to fit a model of the insect’s sensorimotor response empirically to data collected in a tethered flight experiment. There is no guarantee, of course, that a model of the sensorimotor response identified under tethered flight conditions will accurately predict the sensorimotor response under free-flight conditions. Nevertheless, having identified such a model, it is always possible to synthesise a complete, testable model of the system in free flight by marrying the model predicting the external forces and moments in Eqs. 16–17 with the Newton-Euler equations of motion for a rigid body. This is done in the following section.

6 Extension to the free-flight case in closed-loop

Extending the state space model in Eqs. 16–17 to the free-flight case necessitates adding several new states to the state vector \mathbf{x} . These new states are needed to describe the motion of the insect’s body, and must be sufficient to determine the free-flight motion dynamics and the visual, aerodynamic, and inertial stimuli that the insect receives as a result of its own self-motion. We will assume that the insect is flying through still air in a fixed visual environment, so that the visual, aerodynamic, and inertial frames of reference can be assumed to coincide, so that we have the kinematic identities $v_{b|v} \equiv v_{b|a} \equiv v_{b|i}$ and $\omega_{b|v} \equiv \omega_{b|a} \equiv \omega_{b|i}$. We will further assume that the principal axis of the variation in luminance is vertical at all times, which means that the vector of Euler angles $\phi_{b|v}$ is sufficient to determine the direction of gravity in the body axes. Thus, we may write the state vector for the sensorimotor response in free-flight hover as the $(15 + r) \times 1$ vector:

$$\mathbf{x}' = \begin{bmatrix} \omega_{b|h} \\ \phi_{b|h} \\ \vdots \\ v_{b|v} \\ \omega_{b|v} \\ \phi_{b|v} \\ \vdots \\ \mathbf{z} \end{bmatrix} \quad (19)$$

in which we have taken the visual frame of reference \mathcal{F}_v as the primary frame of reference with respect to which the motions of the insect's body are specified. Given the central importance of vision in insect flight control [1], this choice is logical as well as convenient.

6.1 Linearized flight mechanics

The first step in building a state-space model of the free-flight dynamics is to establish the equations of motion expressing the linearized flight mechanics. The only external forces and moments acting upon the system are the insect's weight ($m\mathbf{g}$), the aerodynamic force $\mathbf{F} = \mathbf{F}_r + \Delta\mathbf{F}$, and the aerodynamic moment $\mathbf{M} = \mathbf{M}_r + \Delta\mathbf{M}$. We may similarly decompose the insect's weight, resolved in the body axes, as $m\mathbf{g} = m(\mathbf{g}_r + \Delta\mathbf{g})$, where \mathbf{g}_r denotes the gravitational acceleration vector in the reference condition, and m is the insect's body mass. The gravitational acceleration vector \mathbf{g} is given by:

$$\mathbf{g} = \begin{bmatrix} -g \sin \theta \\ g \cos \theta \sin \phi \\ g \cos \theta \cos \phi \end{bmatrix} \quad (20)$$

where $g = 9.81\text{ms}^{-2}$ is the gravitational acceleration, and where the Euler angles $\boldsymbol{\phi}_{b|v} = [\phi, \theta, \psi]^T$ are assumed to have been defined according to a Tait-Bryan sequence. Specifically, the orientation of the body axes $\{x_b, y_b, z_b\}$ is defined by a sequence of rotations that would bring them to their final orientation from an initial orientation parallel to the visual axes $\{x_v, y_v, z_v\}$. According to this sequence, the axes are first rotated through an angle ψ about the z_b -axis to bring the x_b -axis to its final azimuth, are next rotated through an angle θ about the y_b -axis to bring the x_b -axis to its final elevation, and are then rotated through an angle ϕ about the x_b -axis to bring all of the body axes to their final orientation. Here we have assumed that the body axes are fixed so that all of the Euler angles are zero in the reference condition about which the model is linearized. Hence, in the small disturbance case assumed here, we may make use of the trigonometric approximations $\cos \delta \approx 1$ and $\sin \delta \approx \delta$, where δ is any small angle, to linearize Eq. 20 as:

$$\mathbf{g} \approx \begin{bmatrix} -g\theta \\ g\phi \\ g \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ g \end{bmatrix} + \begin{bmatrix} -g & 0 & 0 \\ 0 & g & 0 \\ 0 & 0 & 0 \end{bmatrix} \boldsymbol{\phi}_{b|v} \quad (21)$$

from which it is obvious that:

$$\Delta\mathbf{g} \approx \begin{bmatrix} -g & 0 & 0 \\ 0 & g & 0 \\ 0 & 0 & 0 \end{bmatrix} \boldsymbol{\phi}_{b|v} \quad (22)$$

because $\mathbf{g}_r = [0, 0, g]^T$ in the assumed reference condition. Furthermore, because $\boldsymbol{\phi}_{b|v}$ is identically zero in the assumed reference condition, the linearized Euler angle rates $\dot{\boldsymbol{\phi}}_{b|v}$ may be equated with the angular velocity components $\boldsymbol{\omega}_{b|v}$, so that we also have the approximation:

$$\dot{\boldsymbol{\phi}}_{b|v} \approx \boldsymbol{\omega}_{b|v} \quad (23)$$

Since we have assumed an equilibrium reference condition, it obviously follows that $\mathbf{F}_r + \mathbf{g}_r = \mathbf{0}$ and $\mathbf{M}_r = \mathbf{0}$. Hence, assuming that the mass distribution properties of the insect can be treated as constant, which is a reasonable first approximation if the mass of the wings is small with respect to the mass of the body, then we may use the Newton-Euler equations for a rigid body to write:

$$\Delta\mathbf{F} + m\Delta\mathbf{g} = m\dot{\mathbf{v}}_{b|v} + \boldsymbol{\omega}_{b|v} \times m\mathbf{v}_{b|v} \quad (24)$$

$$\Delta \mathbf{M} = \mathbf{J} \dot{\boldsymbol{\omega}}_{b|v} + \boldsymbol{\omega}_{b|v} \times \mathbf{J} \boldsymbol{\omega}_{b|v} \quad (25)$$

where \mathbf{J} is an inertia matrix. Since we have assumed that the y_b -axis is normal to the insect's plane of symmetry, the inertia matrix has the form:

$$\mathbf{J} = \begin{bmatrix} I_x & 0 & -I_{xz} \\ 0 & I_y & 0 \\ -I_{xz} & 0 & I_z \end{bmatrix} \quad (26)$$

where $\{I_x, I_y, I_z\}$ are the moments of inertia about the $\{x_b, y_b, z_b\}$ axes, and where I_{xz} is the only non-zero cross-product of inertia. In the linearized case, where $\boldsymbol{\omega}_{b|v}$ and $\mathbf{v}_{b|v}$ represent small disturbance quantities from an equilibrium reference condition, all of the cross-coupling terms vanish from Eqs. 24–25, such that:

$$\dot{\mathbf{v}}_{b|v} \approx m^{-1} \Delta \mathbf{F} + \Delta \mathbf{g} \quad (27)$$

$$\dot{\boldsymbol{\omega}}_{b|v} \approx \mathbf{J}^{-1} \Delta \mathbf{M} \quad (28)$$

With Eqs. 22–23 and 27–28 in hand, we have all of the linearized flight mechanics equations needed to write down a state-space model for the free-flight dynamics in closed loop.

6.2 State-space model of the free-flight dynamics in closed-loop

We may write down a state-space model for the predicted free-flight dynamics by combining the state-space model of the sensorimotor response in tethered flight (Eqs. 16–17) with the linearized Newton-Euler equations (Eqs. 27–28), the linearized equation for the gravitational acceleration vector (Eq. 22), the linearized equation for the Euler angle rates (Eq. 23), and the identities $\mathbf{v}_{b|v} \equiv \mathbf{v}_{b|a} \equiv \mathbf{v}_{b|i}$ and $\boldsymbol{\omega}_{b|v} \equiv \boldsymbol{\omega}_{b|a} \equiv \boldsymbol{\omega}_{b|i}$ given earlier. Solving for the free-flight state vector \mathbf{x}' yields the following state-space model for the free-flight dynamics in closed-loop:

$$\begin{bmatrix} \dot{\boldsymbol{\omega}}_{b|h} \\ \dot{\boldsymbol{\phi}}_{b|h} \\ \mathbf{v}_{b|v} \\ \dot{\boldsymbol{\omega}}_{b|v} \\ \dot{\boldsymbol{\phi}}_{b|v} \\ \dot{\mathbf{z}} \end{bmatrix} = \begin{bmatrix} \mathbf{A}_{11} & \mathbf{A}_{12} & \mathbf{B}_{14} & \mathbf{B}_{15} & \mathbf{0} & \mathbf{A}_{13} \\ \mathbf{I} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & m^{-1} \mathbf{D}_{14} & m^{-1} \mathbf{D}_{15} & \mathbf{G} & m^{-1} \mathbf{C}_{13} \\ \mathbf{0} & \mathbf{0} & \mathbf{J}^{-1} \mathbf{D}_{24} & \mathbf{J}^{-1} \mathbf{D}_{25} & \mathbf{0} & \mathbf{J}^{-1} \mathbf{C}_{23} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I} & \mathbf{0} \\ \mathbf{A}_{31} & \mathbf{A}_{32} & (\mathbf{B}_{31} + \mathbf{B}_{34}) & (\mathbf{B}_{32} + \mathbf{B}_{35} + \mathbf{B}_{36}) & \mathbf{B}_{33} & \mathbf{A}_{33} \end{bmatrix} \begin{bmatrix} \boldsymbol{\omega}_{b|h} \\ \boldsymbol{\phi}_{b|h} \\ \mathbf{v}_{b|v} \\ \boldsymbol{\omega}_{b|v} \\ \boldsymbol{\phi}_{b|v} \\ \mathbf{z} \end{bmatrix} \quad (29)$$

where:

$$\mathbf{G} = \begin{bmatrix} -g & 0 & 0 \\ 0 & g & 0 \\ 0 & 0 & 0 \end{bmatrix} \quad (30)$$

and where it is implicit that the insect is commanding an equilibrium reference condition, which we have assumed here to be a state of hover. It is an open question whether the state-space model in Eq. 29 will accurately predict the free-flight dynamics of an insect, when parameterized on the basis of measurements made in tethered flight. The implicit or explicit assumption of most tethered-flight studies is that this is indeed the case [2, 3], but an important benefit of writing down Eq. 29 is to make clear exactly what is being assumed when interpreting the results of a tethered flight experiment. That is to say, within an LTI modelling framework, the question of whether measurements of an insect's sensorimotor response in tethered flight can be used to infer the insect's sensorimotor response in free-flight hinges upon the empirical question of whether Eq. 29 accurately predicts the insect's free flight dynamics in closed-loop.

Eq. 29 represents the closed-loop dynamics of the sensorimotor response in free-flight, but although it is implicit in the model that there is a commanded reference state, we have not shown any feedforward mechanism. This is deliberate, because although it is certainly possible to make

use of Eqs. 16–17 to postulate a feedforward control mechanism, doing so would require us to be explicit about the units of the reference command. It would also require us to postulate a structure for the feedforward controller, modelling the system as a two degree-of-freedom controller [24], for example. This is beyond the scope of the present report, but will be dealt with in a later paper. In any case, Eq. 29 already captures what we mean by the sensorimotor response in free-flight, which relates specifically to feedback, as opposed to feedforward, control.

7 System energy distribution

As explained in Section 4.2, the state \mathbf{x} of a system is a *minimal* set of internal variables which predictably determines the transfer of input energy to output energy through the system’s dynamics. The total energy transferred from input to output through the system’s dynamics is divided by the system’s state into two parts: the *control energy*, arising from the input-state interaction expressed in the state equation (8); and the *observation energy*, arising from the state-output interaction expressed in the output equation (9). The system-theoretic notion of *controllability* formally defines the LTI system’s capability of using the input energy to control the state while the dual notion of *observability* formally defines the LTI system’s capability to observe the state from the output energy [20]. These notions give rise to the important mathematical tools of controllability and observability Gramians, which we begin by discussing in an abstract sense before describing the formally below. The main fundamental and operational properties of the Gramians are summarized in Sections 7.2 and 7.3 below, in order to give proper insights and precise description of how the state of a system distributes energy among control and observation.

The robustly-computable Gramians, which are $n \times n$ symmetric matrices with real entries, not only indicate *whether* the system is controllable and/or observable, but—crucially—give a quantitative characterisation of *how* the state distributes the energy among control and observation. Specifically, the robustly-computable eigenvectors $\mathbf{v}_{c,1}, \mathbf{v}_{c,2}, \dots, \mathbf{v}_{c,n}$ of the controllability Gramian \mathbf{W}_c give the n orthogonal directions in the n -dimensional state space along which the input energy has the greatest control effect on the state. These most controllable directions $\mathbf{v}_{c,i}$, for $i = 1, 2, \dots, n$, can be automatically ordered so that the greatest amount of the control energy is carried along $\mathbf{v}_{c,1}$ and the least amount of the control energy is carried along $\mathbf{v}_{c,n}$. Dually, the robustly-computable eigenvectors $\mathbf{v}_{o,1}, \mathbf{v}_{o,2}, \dots, \mathbf{v}_{o,n}$ of the observability Gramian \mathbf{W}_o give the n orthogonal directions in the n -dimensional state space along which the observation energy allows the most effective observation of the state. These most observable directions $\mathbf{v}_{o,i}$, for $i = 1, 2, \dots, n$, can be automatically ordered so that the greatest amount of the observation energy is carried along $\mathbf{v}_{o,1}$ and the least amount of the observation energy is carried along $\mathbf{v}_{o,n}$.

It follows that the controllability directions $\mathbf{v}_{c,1}, \mathbf{v}_{c,2}, \dots, \mathbf{v}_{c,n}$ and observability directions $\mathbf{v}_{o,1}, \mathbf{v}_{o,2}, \dots, \mathbf{v}_{o,n}$ define dynamically meaningful directions in the n -dimensional state space. They are therefore of particular interest in the context of formalizing the mode sensing hypothesis, which we interpret here as the general proposition that *the high performance observed in insect flight can be related to the way in which the insect represents its flight dynamics in the physiological system generating its sensorimotor response*. Thus, in the specific context of our state-space model of a tethered insect’s sensorimotor response (16)–(17), the eigenvectors of the controllability Gramian \mathbf{W}_c define the n orthogonal directions in the state space along which visual, aerodynamic, and inertial stimuli corresponding to the insect’s own self motion have the greatest control effect on the internal physiological and kinematic state of the system. Dually, the eigenvectors of the observability Gramian \mathbf{W}_o define the n orthogonal directions in the n -dimensional state space along which the forces and moments that the flight apparatus produces allow the most effective observation of the internal physiological and kinematic state of the system.

7.1 Lyapunov functions

The sensorimotor response of a flying insect is a result of the animal's closed-loop feedback control, and necessarily achieves stable flight. Tethering the insect eliminates its flight dynamics, and may change the equilibrium point of the system, but does not make output of the flight motor unstable. Hence, the developments in the sections below are focused on systems which are stable in the sense of Lyapunov [25]. The essence of the Lyapunov approach is to associate with the system dynamics, or equation (8) in the LTI context, an energy-like function V and to show that this function decreases along the trajectories of the system. More precisely, the Lyapunov function V is a scalar function of state $\mathbf{x}(t)$ that is positive definite, and whose time derivative along *all* trajectories of (8) is negative. In other words, $V(\mathbf{x}(t)) > 0$ for all $\mathbf{x}(t)$, and $\dot{V}(\mathbf{x}(t)) < 0$ for all $\mathbf{x}(t)$ satisfying (8) for $t > 0$. If a Lyapunov function V can be found, then this means that whenever the LTI system is perturbed from its zero equilibrium, it will return to that equilibrium asymptotically, because the energy of the perturbed system inexorably tends to zero, $\lim_{t \rightarrow \infty} V(\mathbf{x}(t)) = 0$. Such a system is said to be asymptotically stable in the sense of Lyapunov.

In the LTI context, a standard candidate Lyapunov function is given by

$$V(\mathbf{x}) = \mathbf{x}^T \mathbf{P} \mathbf{x}, \quad (31)$$

i.e. a quadratic form which, for a symmetric, positive-definite matrix \mathbf{P} indeed is a positive-definite function. The energy-like character of V in (31) is expressed by the fact that it is a sum of squares of the state-space coordinates, which is best seen by considering \mathbf{P} to be a diagonal positive-definite matrix. For the candidate function (31) to be an actual Lyapunov function, it must also decrease along the trajectories of (8). In other words, the derivative

$$\dot{V}(\mathbf{x}) = (\nabla V(\mathbf{x}))^T \dot{\mathbf{x}} = \mathbf{x}^T \underbrace{(\mathbf{A}^T \mathbf{P} + \mathbf{P} \mathbf{A})}_{-\mathbf{Q}} \mathbf{x} = -\mathbf{x}^T \mathbf{Q} \mathbf{x} \quad (32)$$

must be negative definite, or equivalently the matrix \mathbf{Q} must be positive definite. In the derivation of (32), $\dot{\mathbf{x}} = \mathbf{A} \mathbf{x}$ was used, because LTI stability is independent of input \mathbf{u} , and ∇V in (32) stands for the gradient of V . The Lyapunov function requirements that (31) is positive definite and, at the same time, (32) is negative definite (along the trajectories) can be summarised by the requirement that the algebraic Lyapunov matrix equation

$$\mathbf{A}^T \mathbf{P} + \mathbf{P} \mathbf{A} = -\mathbf{Q} \quad (33)$$

has a positive definite solution \mathbf{P} for all positive definite \mathbf{Q} . Equation (33) is often rewritten as

$$\mathbf{A}^T \mathbf{P} + \mathbf{P} \mathbf{A} + \mathbf{Q} = \mathbf{0} \quad (34)$$

for convenience, where both \mathbf{P} and \mathbf{Q} must be positive definite, symmetric, $n \times n$ matrices with real entries.

7.2 Controllability Gramian

Formally, an LTI system is controllable [21] if there exists a control \mathbf{u} which drives the state of the system (8) from any initial condition $\mathbf{x}_0 = \mathbf{x}(0)$ at time $t = 0$ to any desired state $\mathbf{x}_1 = \mathbf{x}(t_1)$ at a finite time $t_1 > 0$. If the system is controllable, then it is natural to ask what about the most efficient control transferring the system from \mathbf{x}_0 to \mathbf{x}_1 over the time interval $[0, t_1]$. For Lyapunov-stable LTI systems, this optimal control problem can be simplified by asking what minimum-energy control has brought the system to the initial condition, i.e. what would have been the most effective history of the system which is summarised in \mathbf{x}_0 . This leads to the

optimal control problem:

$$\min_{\mathbf{u}} J(\mathbf{u}) \stackrel{\text{def}}{=} \int_{-\infty}^0 \mathbf{u}^T(t) \mathbf{u}(t) dt, \quad \text{with (8) constrained by } \mathbf{x}(0) = \mathbf{x}_0. \quad (35)$$

The performance criterion J in (35) expresses the total control energy required to bring the system from the distant past, $t \rightarrow -\infty$, to the beginning of the observation time, $t = 0$. This energy should be minimised by choosing, from the set of admissible (piecewise continuous) controls \mathfrak{U} , the optimal control \mathbf{u}^* which will act on the state through (8) in order to bring the state at $t = 0$ to the value \mathbf{x}_0 , irrespective of the value of the state in the distant past. Using (10), the optimisation constraint is:

$$\mathbf{x}_0 - \int_{-\infty}^0 e^{-\mathbf{A}t} \mathbf{B} \mathbf{u}(t) dt = \mathbf{0}, \quad (36)$$

so that, by elementary theory of optimal control [26], the Lagrangian is obtained by adjoining constraint (36) to the performance criterion J from (35):

$$L(\mathbf{u}(t), \boldsymbol{\lambda}) = \int_{-\infty}^0 \mathbf{u}^T(t) \mathbf{u}(t) dt + \boldsymbol{\lambda}^T \left(\mathbf{x}_0 - \int_{-\infty}^0 e^{-\mathbf{A}t} \mathbf{B} \mathbf{u}(t) dt \right), \quad (37)$$

where the optimal control \mathbf{u}^* is sought as a vector function of time and the Lagrange multiplier $\boldsymbol{\lambda}^*$ is sought as a vector of real constants. A necessary condition for optimality is that the first variation δL vanish for any variations $\delta \mathbf{u}(t)$ over $(-\infty, 0)$ and for any variations $\delta \boldsymbol{\lambda}$ over \mathbb{R}^n , i.e. $\delta L = 0$ for any $\delta \mathbf{u}(t) \in \mathfrak{U}$ and any $\delta \boldsymbol{\lambda} \in \mathbb{R}^n$. This necessary condition yields the optimal solution:

$$\boldsymbol{\lambda}^* = 2\mathbf{W}_c^{-1} \mathbf{x}_0 \quad (38)$$

$$\mathbf{u}^*(t) = \frac{1}{2} \left(\mathbf{B}^T e^{-\mathbf{A}^T t} \right) \boldsymbol{\lambda}^* \quad (39)$$

$$\mathbf{W}_c = \int_0^\infty e^{\mathbf{A}t} \mathbf{B} \mathbf{B}^T e^{\mathbf{A}^T t} dt \quad (40)$$

$$J(\mathbf{u}^*(t)) = \mathbf{x}_0^T \mathbf{W}_c^{-1} \mathbf{x}_0, \quad (41)$$

where the property

$$\int_{-\infty}^0 e^{-\mathbf{A}t} \mathbf{B} \mathbf{B}^T e^{-\mathbf{A}^T t} dt = \int_0^\infty e^{\mathbf{A}t} \mathbf{B} \mathbf{B}^T e^{\mathbf{A}^T t} dt$$

was used; this property holds due to the LTI character of the system.

Hence, in the deterministic setting, the LTI controllability Gramian \mathbf{W}_c of a Lyapunov-stable system (8) has the following key properties:

C-1 \mathbf{W}_c is a symmetric, positive-definite matrix with real entries.

This property follows directly from (40).

C-2 \mathbf{W}_c has real, positive eigenvalues which can be ordered:

$$\lambda_{c,1} \geq \lambda_{c,2} \geq \dots \geq \lambda_{c,n} > 0 \quad (42)$$

and are not necessarily distinct.

This property follows directly from property C-1, because it is a standard property of symmetric, positive-definite matrices.

C-3 W_c defines an ellipsoid in the state space whose semi-axes correspond to the eigenvectors $v_{c,i}$, $i = 1, 2, \dots, n$, of W_c ; furthermore, the lengths of the semi-axes are given by the $\sqrt{\lambda_{c,i}}$, $i = 1, 2, \dots, n$, where $\lambda_{c,i}$, $i = 1, 2, \dots, n$, are the corresponding eigenvalues of W_c .

This property follows from properties C-1 and C-2 by considering the n -dimensional ellipsoid as the set

$$E_c = \{x \in \mathbb{R}^n \mid x^T W_c^{-1} x \leq 1\} \quad (43)$$

for bounded controls $\|u\| \leq 1$, where W_c^{-1} also is a symmetric, positive-definite matrix by virtue of C-1. The semi-axes of the controllability ellipsoid E_c define n orthogonal directions in the n -dimensional state space along which the input energy has most control effect on the state. Furthermore, the input energy effect is graded by the ordering of the eigenvectors of W_c and is quantified by the eigenvalues of W_c . More specifically, $v_{c,1}$ is the most effective direction and the strength of controllability along $v_{c,1}$ is given by $\sqrt{\lambda_{c,1}}$. At the other extreme, $v_{c,n}$ is the least effective direction and the strength of controllability along $v_{c,n}$ is given by $\sqrt{\lambda_{c,n}}$.

C-4 W_c defines the minimum control energy $x_0^T W_c^{-1} x_0$ required to drive the system to the state x_0 from any other state.

This property follows directly from (41).

C-5 W_c satisfies the algebraic Lyapunov equation:

$$A^T W_c + W_c A + B B^T = 0, \quad (44)$$

where A and B come from (8).

This property readily follows by substituting (40) into (44) and noting, by comparing with (34), that (44) indeed is an algebraic Lyapunov equation.

C-6 W_c defines the “required supply” storage function $S_{\text{req}}(x_0) = x_0^T W_c^{-1} x_0$.

This property arises from a generalised concept of the Lyapunov function [27], [28], applicable to systems with inputs and outputs. For a dissipative system (a generalisation of a Lyapunov-stable system [29]) the change in internal energy storage can never exceed what is supplied to the system. Any internal storage function S is bounded by the available storage and the required supply, according to the inequality

$$0 \leq S_{\text{avail}}(x_0) \leq S(x_0) \leq S_{\text{req}}(x_0).$$

It follows from (41) that $x_0^T W_c^{-1} x_0$ is the minimum energy that needs to be supplied to the system to drive it to x_0 from any other state. Hence, this input energy is also the required supply $S_{\text{req}}(x_0) = x_0^T W_c^{-1} x_0$, see [30], [31].

Properties C-1 to C-6 of the controllability Gramian W_c were derived for a stable, *deterministic* LTI system (8). An additional, useful [32] interpretation of W_c is possible in the stochastic set-up and this is now done for completeness. Consider the input-state equation of an LTI system which receives no deterministic input, but—instead—is excited by a p -dimensional vector of zero-mean, white, Gaussian noise w :

$$\dot{x}(t) = A x(t) + B w(t), \quad x(0) = x_0, \quad (45)$$

where, as before, \dot{x} stands for differentiation of state x with respect to time t , while matrices A and B have constant, real entries and have dimensions: $n \times n$, $n \times p$. It is further assumed

that initial condition \mathbf{x}_0 is a vector of random variables and that noise \mathbf{w} has the constant (time-invariant) covariance matrix $\mathbf{V} = \mathcal{E}[\mathbf{w}\mathbf{w}^T]$, where $\mathcal{E}[\cdot]$ stands for the expectation operator.

Since the system (45) is excited by a stochastic input, its state \mathbf{x} will also be a stochastic process, so the covariance matrix of the state, $\mathbf{R}(t) = \mathcal{E}[\mathbf{x}(t)\mathbf{x}^T(t)]$, is well defined. The state covariance matrix is expressed by [33]:

$$\mathbf{R}(t) = \underbrace{e^{At}\mathbf{R}(0)e^{A^T t}}_{\text{excitation due to } \mathbf{x}_0} + \overbrace{\int_0^t e^{A(t-\tau)}\mathbf{B}\mathbf{V}\mathbf{B}^T e^{A^T(t-\tau)} d\tau}^{\text{excitation due to } \mathbf{w}(t)}, \quad (46)$$

where $\mathbf{R}(0) = \mathcal{E}[\mathbf{x}_0\mathbf{x}_0^T]$. For a Lyapunov-stable system, the limit $\lim_{t \rightarrow \infty} \mathbf{R}(t) = \mathbf{R}$ exists and is given by:

$$\mathbf{R} = \int_0^\infty e^{At}\mathbf{B}\mathbf{V}\mathbf{B}^T e^{A^T t} dt \quad (47)$$

(because the influence of the excitation due to \mathbf{x}_0 will become asymptotically negligible) and also satisfies the algebraic matrix equation:

$$\mathbf{A}^T \mathbf{R} + \mathbf{R} \mathbf{A} + \mathbf{B}\mathbf{V}\mathbf{B}^T = \mathbf{0}. \quad (48)$$

Hence, the state covariance matrix $\mathbf{R} = \lim_{t \rightarrow \infty} \mathbf{R}(t)$ is the stochastic counterpart of the deterministic controllability Gramian \mathbf{W}_c , albeit additionally weighted by the input noise covariance matrix \mathbf{V} , as can be seen by comparing (47) with (40) and (48) with (44). The additional presence of the noise covariance matrix \mathbf{V} in (47) and (48) is necessary, because \mathbf{V} expresses the stochastic character of input \mathbf{w} in (45) and was thus absent in (8) for deterministic input \mathbf{u} .

7.3 Observability Gramian

Observability is the problem of determining the value of the state vector knowing only the output over some interval of time. Formally, an LTI system is observable [21] if there exists a finite time $t_1 > 0$ such that, for *any* input \mathbf{u} known on $[0, t_1]$, it is possible to determine the initial condition $\mathbf{x}_0 = \mathbf{x}(0)$ of the system from the corresponding output \mathbf{y} observed on $[0, t_1]$. The emphasis on the reconstruction of the initial condition is motivated by the fact [20] that, if \mathbf{x}_0 can be recovered, then the state $\mathbf{x}(t)$ at any time $t > 0$ can be calculated by solving (8)–(9).

The output energy [34] of an LTI system is defined as:

$$E_o(t) = \int_0^t \mathbf{y}^T(t) \mathbf{y}(t) dt \quad (49)$$

and, for an observable system this output energy must be finite. In particular, it is useful to consider the total observed energy:

$$E_o = \lim_{t \rightarrow \infty} E_o(t) = \int_0^\infty \mathbf{y}^T(t) \mathbf{y}(t) dt. \quad (50)$$

Since LTI observability must hold for any input \mathbf{u} , the zero input can be assumed, $\mathbf{u}(t) = \mathbf{0}$ for all $t > 0$, so that

$$\mathbf{y}(t) = \mathbf{C} e^{At} \mathbf{x}_0 \quad (51)$$

and thus any effects observed in the output must be due to the initial condition only. The total observed energy is given by:

$$E_o = \mathbf{x}_0^T \left(\int_0^\infty e^{A^T t} \mathbf{C}^T \mathbf{C} e^{At} dt \right) \mathbf{x}_0 \quad (52)$$

$$= \mathbf{x}_0^T \mathbf{W}_o \mathbf{x}_0, \quad (53)$$

where

$$\mathbf{W}_o = \int_0^\infty e^{\mathbf{A}^T t} \mathbf{C}^T \mathbf{C} e^{\mathbf{A} t} dt \quad (54)$$

is the observability Gramian for (8)–(9).

Hence, in the deterministic setting, the LTI observability Gramian \mathbf{W}_o of a Lyapunov-stable system (8)–(9) has the following main properties useful for modelling the optomotor response:

O–1 \mathbf{W}_o is a symmetric, positive-definite matrix with real entries.

This property follows directly from (54).

O–2 \mathbf{W}_o has real, positive eigenvalues whose inverses can be ordered:

$$\lambda_{o,1}^{-1} \geq \lambda_{o,2}^{-1} \geq \dots \geq \lambda_{o,n}^{-1} > 0 \quad (55)$$

and are not necessarily distinct.

This property follows directly from property O–1, because it is a standard property of symmetric, positive-definite matrices.

O–3 \mathbf{W}_o defines an ellipsoid in the state space whose semi-axes correspond to the eigenvectors $\mathbf{v}_{o,i}$, $i = 1, 2, \dots, n$, of \mathbf{W}_o ; furthermore, the lengths of the semi-axes are given by the $1/\sqrt{\lambda_{o,i}}$, $i = 1, 2, \dots, n$, where $\lambda_{o,i}$, $i = 1, 2, \dots, n$, are the corresponding eigenvalues of \mathbf{W}_o .

This property follows from properties O–1 and O–2 by considering the n -dimensional ellipsoid as the set

$$\mathbf{E}_o = \{\mathbf{x} \in \mathbb{R}^n \mid \mathbf{x}^T \mathbf{W}_o \mathbf{x} \leq 1\}. \quad (56)$$

The semi-axes of the observability ellipsoid \mathbf{E}_o define n orthogonal directions in the n -dimensional state space along which the output energy allows the most effective observation of the state. Furthermore, the output energy effect is graded by the ordering of the eigenvectors of \mathbf{W}_o and is quantified by the eigenvalues of \mathbf{W}_o . More specifically, $\mathbf{v}_{o,1}$ is the most effective direction and the strength of observability along $\mathbf{v}_{o,1}$ is given by $1/\sqrt{\lambda_{o,1}}$. At the other extreme, $\mathbf{v}_{o,n}$ is the least effective direction and the strength of observability along $\mathbf{v}_{o,n}$ is given by $1/\sqrt{\lambda_{o,n}}$.

O–4 \mathbf{W}_o defines the output energy $\mathbf{x}_0^T \mathbf{W}_o \mathbf{x}_0$ generated by \mathbf{x}_0 in the absence of any input excitation. In other words, E_o in (53) is produced solely from the energy stored by the system, accumulated as a result of its history up to time $t = 0$.

This property follows directly from (50) and (51).

O–5 \mathbf{W}_o satisfies the algebraic Lyapunov equation:

$$\mathbf{A}^T \mathbf{W}_o + \mathbf{W}_o \mathbf{A} + \mathbf{C}^T \mathbf{C} = \mathbf{0}, \quad (57)$$

where \mathbf{A} and \mathbf{C} come from (8)–(9).

This property readily follows by substituting (54) into (57) and noting, by comparing with (34), that (57) indeed is an algebraic Lyapunov equation.

O-6 W_o defines the “available storage” function $S_{\text{avail}}(\mathbf{x}_0) = \mathbf{x}_0^T W_o \mathbf{x}_0$.

This property arises from a generalised concept of the Lyapunov function [27], [28], applicable to systems with inputs and outputs. For a dissipative system (a generalisation of a Lyapunov-stable system [29]) the change in internal energy storage, can never exceed what is supplied to the system. Any internal storage function S is bounded by the available storage and the required supply, according to the inequality

$$0 \leq S_{\text{avail}}(\mathbf{x}_0) \leq S(\mathbf{x}_0) \leq S_{\text{req}}(\mathbf{x}_0).$$

It follows from (52) that $\mathbf{x}_0^T W_o \mathbf{x}_0$ is the total energy due to excitation by \mathbf{x}_0 which can be observed through \mathbf{y} . Hence, this output energy is also the available storage $S_{\text{avail}}(\mathbf{x}_0) = \mathbf{x}_0^T W_o \mathbf{x}_0$, see [30], [31].

Since LTI observability is independent of input, nothing new can be gained by considering a stochastic input like \mathbf{w} in (45). Even if the initial condition \mathbf{x}_0 is allowed to be a random variable, then the expression for the output under zero input (51) remains unchanged and so does the subsequent analysis of the observability Gramian.

7.4 Non uniqueness of the state-space realisation

Empirically, the sensorimotor response of an insect is defined by the experimentally available input-output pairs which, in the context of an LTI system, corresponds directly to the external model in (7). The external model uniquely expresses the experimentally observable input-output behaviour of the integrated system, but its unique input-output behaviour can in turn be realised by infinitely many internal models (8)–(9). This non-unique realisation of a unique input-output behaviour is due to the freedom of choice of the internal state $\mathbf{x}(t)$ in (8)–(9). Indeed, if $\mathbf{x}(t)$ is a set of internal state variables realising the input-output behaviour defined by many input-output pairs, then transformation of this state \mathbf{x} into any other state $\hat{\mathbf{x}}$ will result in equivalent input-output behaviour. This can be seen by defining the state transformation:

$$\hat{\mathbf{x}}(t) = \mathbf{T}\mathbf{x}(t), \quad (58)$$

where \mathbf{T} is any non-singular, $n \times n$ matrix with real entries. Since \mathbf{T} is non-singular, its inverse \mathbf{T}^{-1} exists, so that (58) can be substituted into (8)–(9) to yield the transformed internal LTI model:

$$\dot{\hat{\mathbf{x}}}(t) = \hat{\mathbf{A}}\hat{\mathbf{x}}(t) + \hat{\mathbf{B}}\mathbf{u}(t), \quad \hat{\mathbf{x}}(0) = \hat{\mathbf{x}}_0, \quad (59)$$

$$\mathbf{y}(t) = \hat{\mathbf{C}}\hat{\mathbf{x}}(t) + \hat{\mathbf{D}}\mathbf{u}(t), \quad (60)$$

where the transformed matrices $\hat{\mathbf{A}}$, $\hat{\mathbf{B}}$, $\hat{\mathbf{C}}$ and $\hat{\mathbf{D}}$ are given by:

$$\begin{aligned} \hat{\mathbf{A}} &= \mathbf{T}\mathbf{A}\mathbf{T}^{-1} \\ \hat{\mathbf{B}} &= \mathbf{T}\mathbf{B} \\ \hat{\mathbf{C}} &= \mathbf{C}\mathbf{T}^{-1} \\ \hat{\mathbf{D}} &= \mathbf{D}. \end{aligned} \quad (61)$$

By comparing (8)–(9) with (59)–(60), it can readily be seen that the state transformation (58) does not alter either the input $\mathbf{u}(t)$ or the output $\mathbf{y}(t)$. Thus, both the state $\mathbf{x}(t)$ in (8)–(9) and the state $\hat{\mathbf{x}}(t)$ in (59)–(60) realise the same input-output behaviour. Since the choice of the transformation matrix \mathbf{T} in (58) is arbitrary, it follows that there are infinitely many state-space realisations of a unique input-output behaviour.

It is worth emphasising that, for the same input-output behaviour, each distinct state-space realisation of that behaviour has a distinct state, and distinct system matrices. In other words, if

$\mathbf{x}(t)$ and $\hat{\mathbf{x}}(t)$ are two distinct state-space realisations of the same input-output behaviour, such that $\mathbf{x}(t) \neq \hat{\mathbf{x}}(t)$, then in general the system matrices are also distinct, so that $\mathbf{A} \neq \hat{\mathbf{A}}$, $\mathbf{B} \neq \hat{\mathbf{B}}$, $\mathbf{C} \neq \hat{\mathbf{C}}$. Logically, the system matrices \mathbf{A} , \mathbf{B} , \mathbf{C} must be different for different state-space realisations, because the state $\mathbf{x}(t)$ is a conduit for transferring the input energy to the output energy through the system's dynamics. Hence, if $\mathbf{x}(t)$ is transformed into a different $\hat{\mathbf{x}}(t)$, then \mathbf{A} , \mathbf{B} , \mathbf{C} must be transformed into a correspondingly different $\hat{\mathbf{A}}$, $\hat{\mathbf{B}}$, $\hat{\mathbf{C}}$, because the input energy is transferred to the output energy differently by $\mathbf{x}(t)$ and $\hat{\mathbf{x}}(t)$. In contrast, the direct input-output transmission matrices are always equal, such that $\mathbf{D} = \hat{\mathbf{D}}$, because the state is not involved in the direct transmission of input energy to output energy.

This non-uniqueness of the state-space realisation is potentially problematic if—as here—the basis for defining the internal state of the system is not defined from first principles. Thus, although the issue of selecting a particular state-space realization would not arise in first-principles modelling, where the state of the system is expressed in terms of physically meaningful variables, this issue clearly needs to be addressed when identifying the state vector $\mathbf{x}(t)$ as well as the system matrices \mathbf{A} , \mathbf{B} , \mathbf{C} from experimentally observable input-output pairs. A practical and rational resolution to the problem is provided by selecting the particular state-space realisation of the system that divides the its energy equally between control and observation. The unique state-space realisation that results in equitable system energy distribution between control and observation is known as a balanced realisation, and is of interest here for two reasons: first, because it allows us to identify a unique but non-arbitrary realisation of the state-space model in (8)–(9); and second, because it has a number of appealing theoretical properties which have physical meaning when a realization is implemented in analogue circuitry.

7.5 Equitable system energy distribution

The postulate of equitable system energy distribution between control and observation allows an essentially unique choice from infinitely many state-space realisations of the sensorimotor response. In LTI system-theoretic terms this choice is the *balanced realisation* for which the postulated equitable system energy distribution is achieved by requiring that the input and output energy is balanced [35], [36]. More specifically, for a state-space realisation to be *internally balanced* it is required that a *balanced state* \mathbf{x}_b is chosen such that, for this balanced state \mathbf{x}_b , both Gramians are equal and diagonal:

$$\mathbf{W}_c = \mathbf{W}_o = \text{diag}[\sigma_1, \sigma_2, \dots, \sigma_n] = \begin{bmatrix} \sigma_1 & 0 & \dots & 0 \\ 0 & \sigma_2 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & \sigma_n \end{bmatrix}. \quad (62)$$

Balanced realisation for Lyapunov-stable LTI systems has several remarkable properties, relevant to the postulated mathematical modelling of an insect's sensorimotor response:

B-1 Balanced realisation is unique up to multiplication by a sign matrix.

This property means that any state \mathbf{x}_b , with arbitrary Gramians, can be transformed to a balanced state \mathbf{x}_b by a transformation \mathbf{T}_b through $\mathbf{x}_b = \mathbf{T}_b \mathbf{x}$, see [37]. The balancing transformation matrix \mathbf{T}_b is unique up to multiplication by a sign matrix $\mathbf{S} = \text{diag}[\pm 1, \pm 1, \dots, \pm 1]$, see [36]. In other words, if \mathbf{T}_b is a balancing transformation matrix, then so is $\mathbf{S}\mathbf{T}_b$.

B-2 The eigenvalues of balanced Gramians (62) are real, positive numbers which can be ordered:

$$\sigma_1 \geq \sigma_2 \geq \dots \geq \sigma_n > 0 \quad (63)$$

and are not necessarily distinct.

The eigenvalues of balanced Gramians σ_i , $i = 1, 2, \dots, n$, are the Hankel singular values [38], [36], i.e. the square roots of the eigenvalues of the Hankel matrix \mathbf{H} which is the product of the Gramians \mathbf{W}_o and \mathbf{W}_c , given in any state-space coordinates, $\mathbf{H} = \mathbf{W}_o \mathbf{W}_c$. In other words, $\sigma_i = \sqrt{\lambda_i(\mathbf{H})}$, $i = 1, 2, \dots, n$.

B-3 Balanced realisation maximises energy storage efficiency of the system.

It follows from C-4 and C-6 that $S_{\text{req}}(\mathbf{x}_0) = \mathbf{x}_0^T \mathbf{W}_c^{-1} \mathbf{x}_0$ is the optimal input energy while from O-4 and O-6 it follows that $S_{\text{avail}}(\mathbf{x}_0) = \mathbf{x}_0^T \mathbf{W}_o \mathbf{x}_0$ is the optimal output energy. The energy storage efficiency defined as [39]

$$\eta(\mathbf{x}_0) = \frac{S_{\text{avail}}(\mathbf{x}_0)}{S_{\text{req}}(\mathbf{x}_0)} = \frac{\mathbf{x}_0^T \mathbf{W}_o \mathbf{x}_0}{\mathbf{x}_0^T \mathbf{W}_c^{-1} \mathbf{x}_0} \quad (64)$$

is maximised with respect to the initial condition \mathbf{x}_0 when \mathbf{x}_0 is the eigenvector of the Hankel matrix $\mathbf{H} = \mathbf{W}_o \mathbf{W}_c$ associated with the largest Hankel singular value σ_1 , see B-2 above.

B-4 Balanced realisation gives an equitable system energy distribution, evenly dividing the system's energy between control and observation.

This crucial property follows immediately by applying C-3 and O-3 to (62).

8 Mode Sensing Hypothesis

Because of the many favourable properties of a balanced realisation, we postulate that the function of the insect's sensorimotor response is equitable system energy distribution in the integrated system composed of the sensor dynamics, processor dynamics, actuator dynamics, and free-flight motion dynamics. This may be treated as a system theoretic interpretation of the Mode Sensing Hypothesis, although we note that there are other possibilities consistent with the original verbal statement of that hypothesis. For example, in the spirit of [1], the design of the sensors might be supposed to be matched to certain of the eigenvectors of the system matrix in the free-flight case in closed-loop (Eq. 29). Ultimately, however, the Mode Sensing Hypothesis can be understood as the statement that there is a common principle underlying the organization of feedback control systems in flying insects. If such a principle exists, then it ought to be possible to express it using the system theoretic concepts of observability and controllability that we have examined above. The hypothesis that insects implement their sensorimotor response under a balanced realisation is one possible expression of just such a principle. A rigorous scientific test of this hypothesis would be to demonstrate that the internal physiological states \mathbf{z} that are identified by assuming a balanced realization correspond to 'discoverable' internal physiological states in the real insect. That is to say, the insect itself embodies a realization of the state space model, and so if that 'true' realization is correctly identified then: a) the states of the identified model should be physically meaningful; and b) the structure of the Jacobian matrices in this realization should relate directly to the physical architecture of the insect's control system. Thus, if there is indeed a common principle underlying the organization of feedback control systems in flying insects then we will know that we have identified that principle correctly when conditions (a) and (b) are satisfied under that principle across a range of different species.

9 Conclusions

We have laid out the necessary mathematical framework above for formulating an empirically testable control theoretic interpretation of the Mode Sensing Hypothesis. Key novelties of the approach include:

1. top-down application of the state-space representation to a sensorimotor response operating in closed-loop, in contrast to the bottom-up approach of starting with an open-loop description of the insect's flight dynamics, and postulating closure of the assumed control loop(s) by sensory feedback;
2. complete specification of the input and output vectors associated with an insect's sensorimotor response, in contrast to previous work in which input and output have been defined in an *ad hoc* manner;
3. a system theoretic interpretation of the Mode Sensing Hypothesis, wherein we postulate that the function of the insect's sensorimotor response is equitable system energy distribution in the integrated system composed of the sensory and neural processing apparatus, the flight apparatus, and the flight motion dynamics.

The results that we have presented assume the use of a linear time-invariant (LTI) framework, which we justified at the outset on the basis that insect sensorimotor responses may be expected to be time-invariant over an intermediate range of timescales, noting that a linearized model is only expected to be valid for disturbances of limited angular speed and range. Although we have not discussed any further specialisations or generalisations of the standard LTI systems theory, we note in passing that the LTI theory of balanced realisations has a useful specialisation involving frequency-weighted Gramians [40, 41, 30] which could provide a new way of interpreting the bandwidth hierarchy of insect sensors. Conversely, the framework that we have outlined above generalises in a reasonably straightforward manner to the linear time-variant (LTV) context [42]. Generalisation to the nonlinear case represents a much greater challenge for at least three reasons: (i) the nonlinear theory of balanced realisations is much less well developed than in the LTI/LTV case; (ii) operationally effective tools (system identification) are much less well developed; (iii) it is not immediately obvious whether nonlinear models from (i) may be expected to capture the essential nonlinearity of insect flight dynamics and control. Finally, although we defer discussion of subspace identification methods to a later paper, the framework that we have outlined is operationally effective for inferring the proposed models from experimental data [22, 23, 43, 44, 45]. A short bibliography is provided overleaf as a guide to some of the wider relevant literature.

10 Bibliography

Gramians: [21], [33], [34], [39], [31], [46], [47], [48], [49], [50]

Gramian assignment: [32], [51], [52], [53]

Gramian-based input-output choice: [54], [55], [56], [57]

Lyapunov equation: [58], [59], [60], [61]

Balanced realisations:

LTI: [35], [62], [63]

LTI, frequency-weighted: [40], [41], [30]

LTV: [42]

nonlinear: [64], [65]

Hankel singular values: [38], [66]

Model reduction (balanced truncation): [36], [67], [68], [69]

Model aggregation: [70]

SIM: [22], [23], [43], [44], [45]

11 Acknowledgments

We thank our sponsors for giving us the opportunity to explore this topic in depth, and thank Ric Wehling and Gregg Abate in particular for their interest and support. Effort sponsored by the Air Force Office of Scientific Research, Air Force Materiel Command, USAF, under grant number FA8655-13-1-3077. The U.S. Government is authorized to reproduce and distribute reprints for Governmental purpose notwithstanding any copyright notation thereon. The research leading to these results has received funding from the European Research Council under the European Community's Seventh Framework Programme (FP7/2007-2013)/ERC grant agreement no. 204513.

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